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The influence of the mandibles of Diplopoda on the food — a dependence of fine structure and assimilation efficiency

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With 6 figures

1. Introduction

Since the role of soil animals in decomposition is still insufficiently understood (Hågvar, 1988), it is necessary that the specific mechanisms, by which decomposers function within the soil subsystem, be investigated more intensely (for reviews see: Dickinson & Pugh, 1974; Seastedt, 1984). Considering growing problems in soil pollution, a better understanding is urgently needed.

Diplopoda are among the most important decomposition-enhancing soil animals (Edwards, 1974; Schaefer, 1988; Striganova, 1971). They have thus been subject to numerous studies on soil ecology, including ecophysiology (Anderson & Bignell, 1982; Bocock, 1963; Wittassek, 1987; Wooten & Crawford, 1975). However, these studies have not yet been linked to morphological aspects. Notwithstanding these many studies, there is — as with other soil animals — a great lack in knowledge of the specific ability of soil animals to integrate into the soil system.

According to Anderson & Bignell (1982), Gere (1956), Kayed (1978), Kondeva (1980), Pokarzhevskii (1981), Striganova & Rachmanov (1972), Striganova & Valiachmedov 1976), Wooten (1974), and Wooten & Crawford (1975) various diplopod species are characterized by different assimilation rates. In the present study, 8 species were compared with regard to their assimilation rates and it was questioned to what mechanisms these differences could be ascribed.

It has been known for a long time that the relative consumption and the assimilation rate of arthropods decreases with increasing body size (e.g.Berthet, 1971; Kondeva, 1980; Striganova, 1972). This fact could possibly be related to a higher litter-exploitation rate of the smaller animals.

Since the mandibles of diplopods evidently are highly complex organs (Enghoff, 1979; Köhler & Alberti, 1990) and the only masticating structures, it was hypothesized that they are responsible for the different assimilation efficiencies.

2. Material and methods

Adults of the following species were examined: *Glomeris marginata* (Villers, 1789) (Glomeridae), *Craspedosoma alemannicum* Verhoeff, 1910 (Craspedosomatidae), *Mycogona germanica* (Verhoeff, 1897) [Chordeumatidae], *Polydesmus angustus* Latzel, 1884 (Polydesmidae), *Julus scandinavius* Latzel, 1884; *Cylindroiulus silvarum* (Meinert, 1868); *Ommatoiulus rutilans* (C. L. Koch, 1847), and *Tachypodoiulus albipes* (C. L. Koch, 1838) [Iulidae].

Specimens (number in brackets) of *G. marginata* (13 animals), *C. alemannicum* (39), *M. germanica* (10), *P. angustus* (6), *J. scandinavius* (9), *C. silvarum* (7), *O. rutilans* (4), and *T. albipes* (4) were kept individually in plastic boxes on a ground of plaster of Paris, which was constantly held moist. The specimens were fed half-year old

leaf litter pieces of *Fagus sylvatica*, *Castanea sativa*, *Quercus petraea*, and *Quercus rubra* at a temperature of 15°C. Since this food had not been sterilized, the effect of the microbial activity has been considered. Therefore, leaf litter of the tree species mentioned above was cultivated in plastic boxes under the same conditions, but without any contact to faunal components. The mass deficiency obtained under these circumstances was measured. The real ingested litter mass M_N [mg] is then represented by

$$M_N \text{ [mg]} = \sum_{i=1}^{n} \frac{(\Delta M \text{ [\%]} - \Delta m_z \text{ [\%]}) \cdot m_0 \text{ [mg]}}{100 \text{ [\%]}}$$

(ΔM [%] = percental, total mass deficiency of the leaf litter caused by both microbial and diplopod activity, Δm_z [%] = percental mass deficiency of the litter caused by microbial activity only, m_0 [mg] = mass of litter at the time of 0, n = number of litter pieces).

The faeces were collected daily, oven-dried, and weighed. The mass assimilation rate A_m [%] is calculated by

$$A_m \text{ [\%]} = 100 \text{ [\%]} - \left(\frac{M_F \text{ [mg]}}{M_N \text{ [mg]}} \cdot 100 \text{[\%]} \right)$$

(M_F [mg] = total faecal mass).

Since *O. rutilans*, *J. scandinavius*, and (partly) *T. albipes* did not accept the food, the essay was repeated with further decomposed leaf litter. The microbially caused mass deficiency of this litter material was measured in a separate essay as well.

For scanning electron microscopy (SEM), the mandibles were prepared by dehydration in 70%, 95%, and 100% ethanol. Subsequently, they were transferred into dichlor-difluormethane, critical-point dried, mounted on Al-stubs, and coated with gold (ROSENBAUER & KEGEL, 1978). Furthermore samples of the faeces of all species mentioned above were oven-dried, mounted, and coated in the same way. Scanning electron microscope: PHILIPS SEM505.

3. Results

3.1. Nutrition

The different sorts of leaf litter examined showed different palatabilities. The two species of *Quercus*, which were ingested in similar quantities, were less attractive than *C. sativa*. The least attractive species was *F. sylvatica*. The relative ingestion rate of the litter species are shown in fig. 1. These differences in food preference correlate with the mass deficiency caused by microbial activity, which was highest in *C. sativa* and − not regarding the further decomposed litter − lowest in *F. sylvatica* (fig. 2).

The assimilation rate of the smallest species was the highest of all the examined genera. More than half of the mass of the ingested material was assimilated by these animals. The exact data are shown in fig. 6. The big iulid species *T. albipes*, *O. rutilans*, and *J. scandinavius* showed the lowest assimilation efficiencies. None of them reached the 11% level. The smaller iulid *C. silvarum*, *G. marginata*, and *P. angustus* were intermediate, with assimilation rates between 17 to 31%.

3.2. Morphology

Each mandible of the Diplopoda is divided into three parts, but only the distal part, which has been called gnathal lobe by ENGHOFF (1979) and MANTON (1979), takes part in crushing the food into small pieces. The gnathal lobes act against one another and, therefore, the crushing structures point towards the middle of the oral cavity. The biting apparatus of the diplopod's gnathal lobe consists of the following substructures: the external and internal teeth, which only roughly cut the litter particles; the pectinate lamellae; the intermediate area, which bears tiny bristles; and the molar plate, which squeezes the ingested material (ENGHOFF, 1979; KÖHLER & ALBERTI, 1990; VERHOEFF, 1928).

The substructures of the gnathal lobe most likely determining the size of the ingested particles are the teeth of the pectinate lamellae. In each of the examined species these teeth are arranged in a different manner. The iulid species show only 4 pectinate lamellae with a low density of teeth.
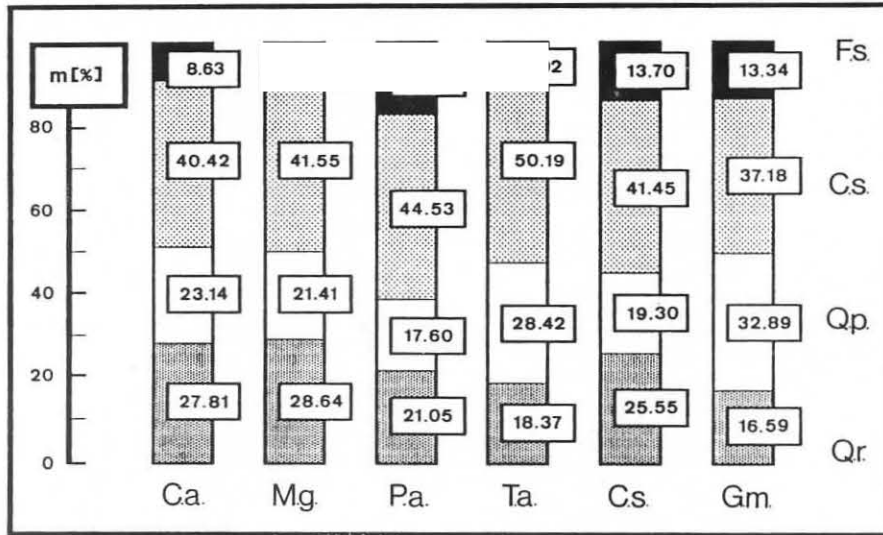
Fig. 1. Relative ingestion rate of the species accepting the half-year old litter pieces of *Fagus sylvatica* (F. s.), *Castanea sativa* (C. s.), *Quercus petraea* (Q. p.), and *Quercus rubra* (Q. r.). C. a.: *Craspedosoma alemannicum*, C. s.: *Cylindroiulus silvarum*, G. m.: *Glomeris marginata*, M. g.: *Mycogona germanica*, P. a.: *Polydesmus angustus*, T. a.: *Tachypodoiulus albipes*, m [%]: percental consumption of litter mass.
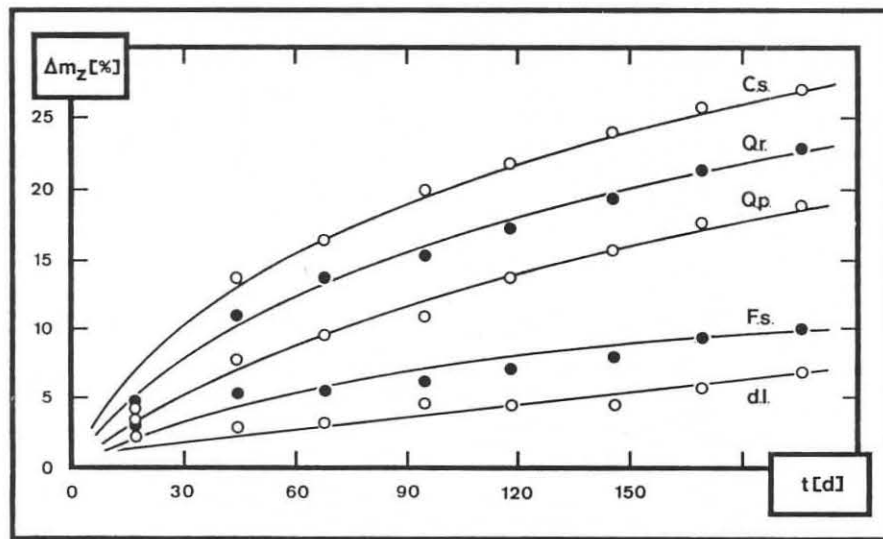

Fig. 2. Percental mass deficiency of the litter caused by microbial activity alone (Δm_z [%]) in dependence of time (t [d]). C. s.: *Castanea sativa*, F. s.: *Fagus sylvatica*, Q. p.: *Quercus petraea*, Q. r.: *Quercus robur*, d. l.: further decomposed litter material.
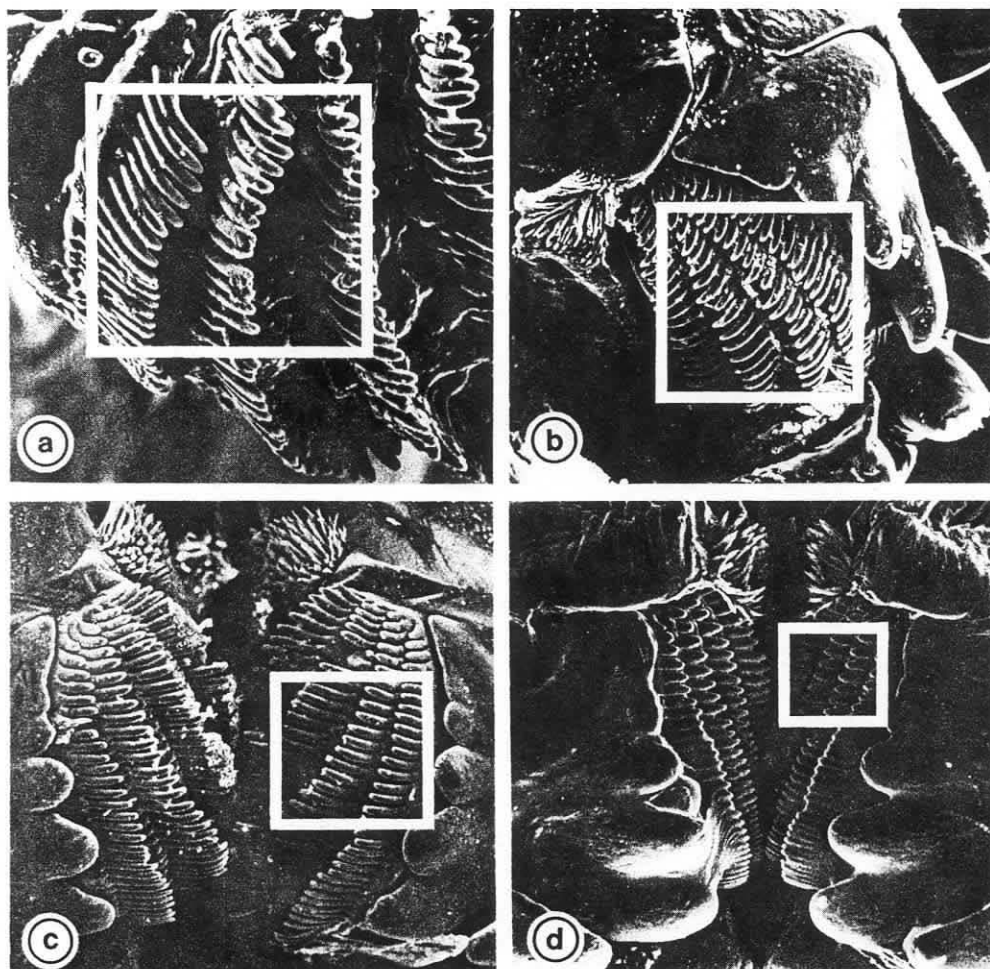
Fig. 3. Pectinate lamellae of the mandible. a: *Tachypodoiulus albipes*, b: *Cylindroiulus silvarum*, c: *Julus scandinavius*, d: *Ommatoiulus rutilans*, squares = 10,000 µm².

In *O. rutilans*, on the average 22 teeth per 10,000 µm² were counted; in *T. albipes* there is an average of 33 teeth per 10,000 µm²; in *J. scandinavius* there are 28. The smaller species *C. silvarum* bears an average of 58 teeth per 10,000 µm² (fig. 3).

Three of the 9 pectinate lamellae of *G. marginata* are characterized by a decreasing number of teeth. However, the remaining 6 show a constant density of 55 teeth per 10,000 µm² on the average.

A similar density of teeth was observed in *P. angustus*. Although only 6 pectinate lamellae exist in this type, the average number of about 60 teeth per 10,000 µm² resembles the situation in *Glomeris*.

The smallest species *M. germanica* and *C. alemannicum* show a much higher density. The 10 pectinate lamellae of *M. germanica* consist of an average of 260 teeth per 10,000 µm². The teeth of *C. alemannicum*, standing in an average density of about 330 per 10,000 µm², form 10 or 11 pectinate lamellae (fig. 4).

Correlating with these observations and the assumed masticating function of the gnathal lobes, the faeces of the compared species showed differences in particle size. Although in each faecal
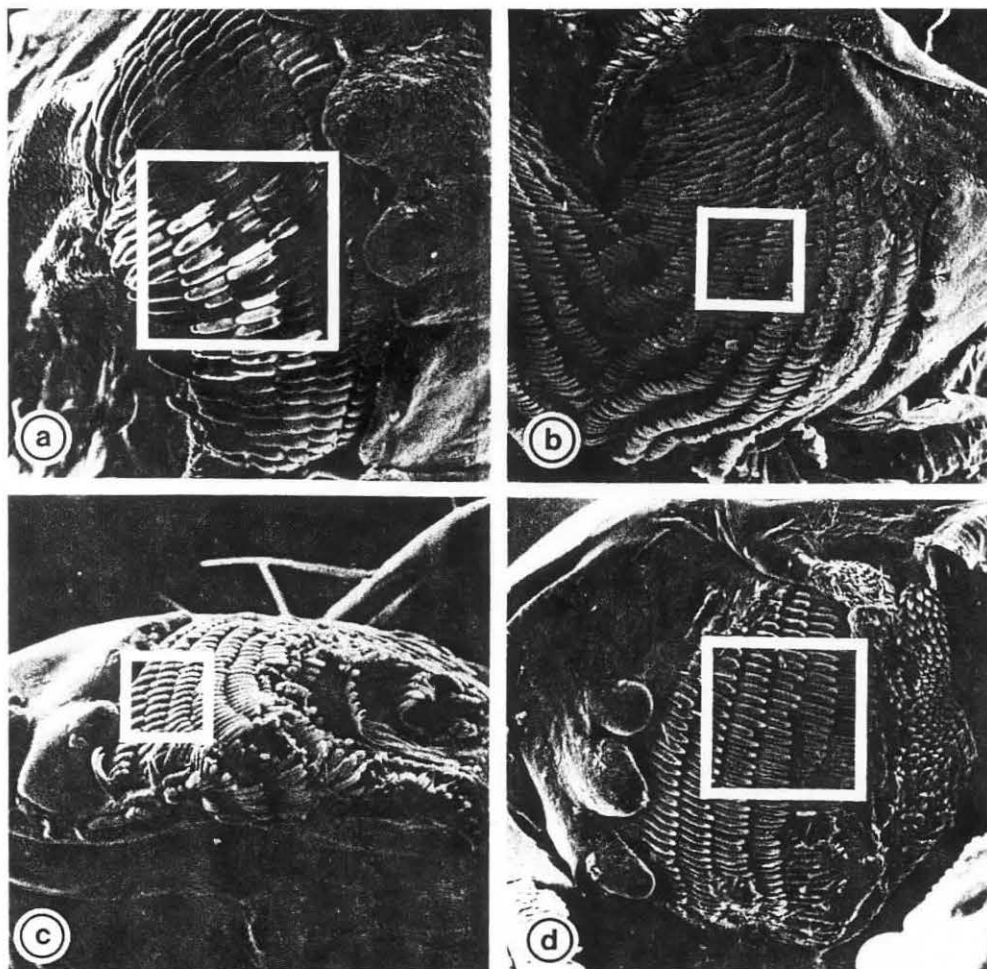
Fig. 4. Pectinate lamellae of the mandible. a: *Glomeris marginata*, square = 10,000 μm², b: *Craspedosoma alemannicum*, square = 1,000 μm², c: *Mycogona germanica*, square = 1,000 μm², d: *Polydesmus angustus*, square = 10,000 μm².

pellet particles varied in size, an obvious tendency was observable: the average particle size was largest in the big iulid species where tooth density is low, and smallest in the smallest species *C. alemannicum* and *M. germanica* where tooth density is highest. The remaining species occupy intermediate positions. Thus decreasing particle sizes correlate with increasing tooth densities in the examined species (fig. 5).
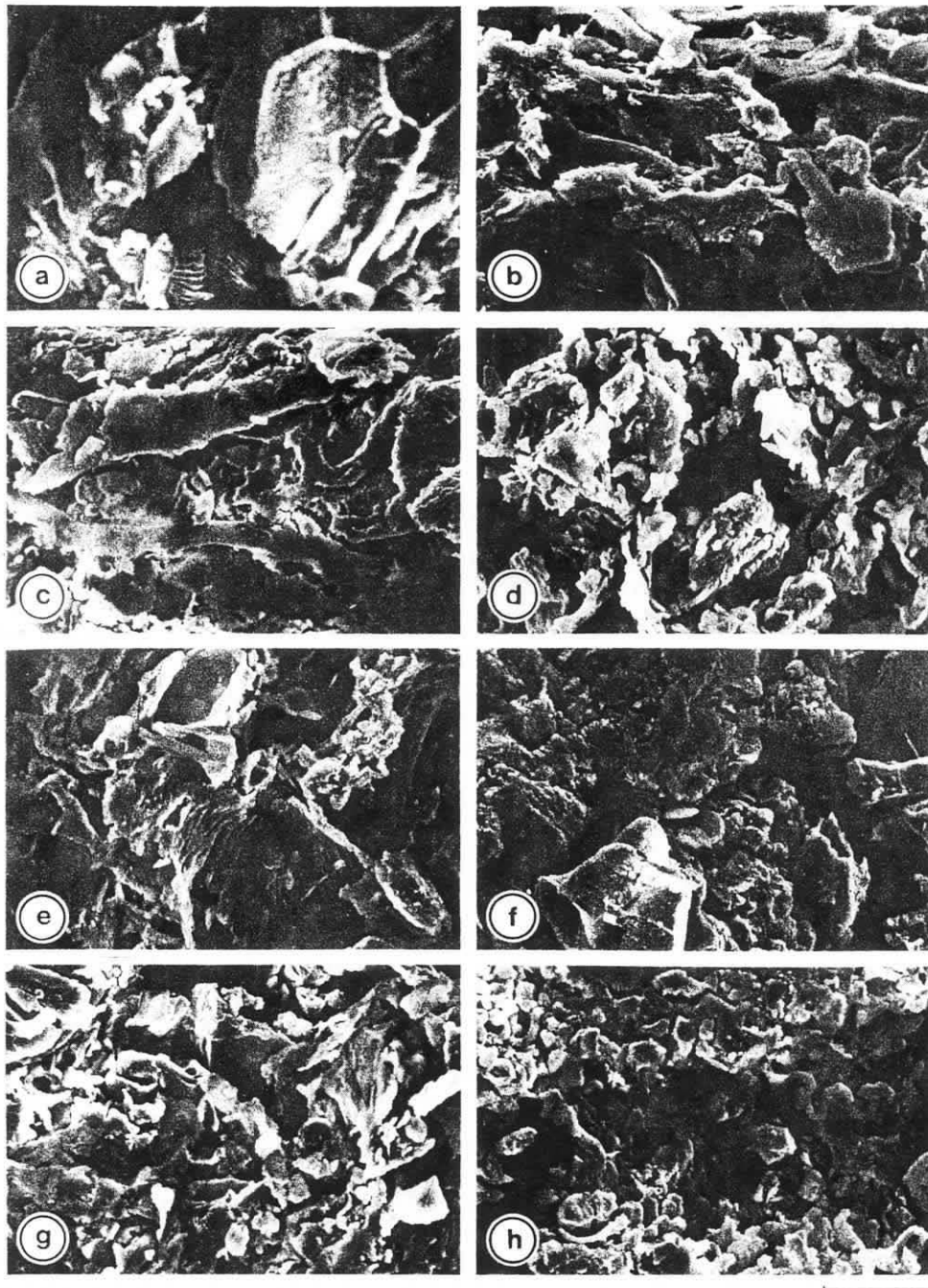
Fig. 5. Faeces particles of the examined species. a: *Tachypodoiulus albipes*, b: *Ommatoiulus rutilans*, c: *Julus scandinavius*, d: *Glomeris marginata*, e: *Cylindroiulus silvarum*, f: *Polydesmus angustus*, g: *Mycogona germanica*, h: *Craspedosoma alemannicum*. Scale bar = 20 μm.
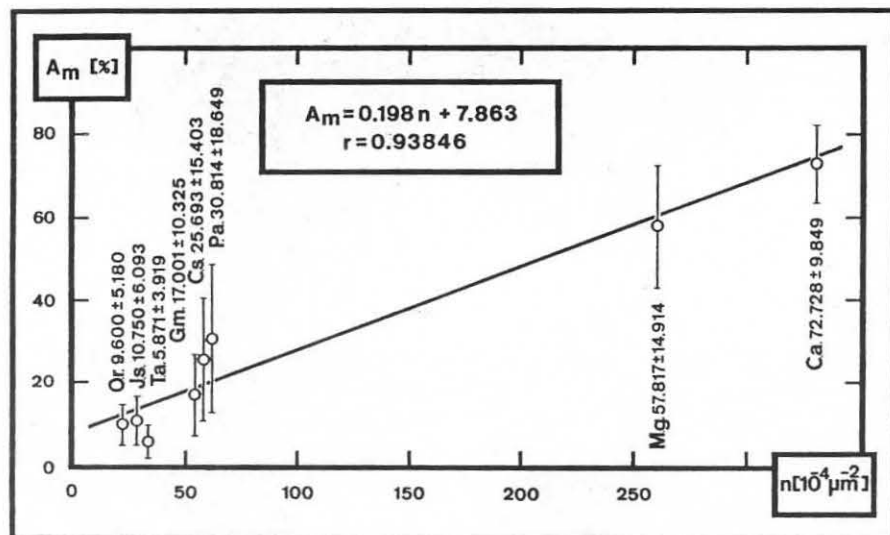
Fig. 6. Dependence and linear regression of teeth density (n $[10^{-4} \ \mu m^{-2}]$) and assimilation rate (A_m [%]) in the examined species. The exact data of assimilation efficiencies are placed near the abbreviations for the particular species: C. a.: *Craspedosoma alemannicum*, C. s.: *Cylindroiulus silvarum*, G. m.: *Glomeris marginata*, J. s.: *Julus scandinavius*, M. g.: *Mycogona germanica*, O. r.: *Ommatoiulus rutilans*, P. a.: *Polydesmus angustus*, and T. a.: *Tachypodoiulus albipes*.

4. Discussion

Since no masticating apparatuses can be found in the rather simple gut of the Diplopoda, mechanical crushing of food can only be ascribed to the mouthparts. It is very likely that the teeth of the pectinate lamellae mesh with one another to cut the food into small pieces (KÖHLER & ALBERTI, 1990). The acceptance of leaf litter by the animals seems not to depend strictly on the litter species. The stage of decomposition appears to be more decisive (BECK & BRESTOWSKI, 1980; SCHMIDT, 1952). According to previous examinations (LYFORD, 1943; NEUHAUSER & HARTENSTEIN,1978; SCHMIDT, 1952), Fagaceae showed a lower palatability to diplopods than the leaves of most other tree species. Moreover, freshly fallen leaves of *Quercus*-species are not attractive for consumption (BECK & BRESTOWSKI, 1980; SCHMIDT, 1952). This may result from a low relative nitrogen content of these leaves. The relative nitrogen content rises with increasing age due to a more rapid loss of non-nitrogeneous leaf constituents, while the amount of nitrogen present in the leaves remains relatively constant (ANDERSON, 1973). The acceptance therefore increases with the degree of decomposition and the correlated decreasing C/N-ratio (BECK & BRESTOWSKI, 1980; SATCHELL & LOWE, 1967; SCHAEFER, 1988). Thus some litter species reach the stage of acceptance and consumption by the macroedaphon much earlier than others (EHLERT, 1980).

The mass assimilation efficiency of diplopods varies with temperature. Though GERE (1956) assigned the optimum of assimilation of central European diplopods to only a few degrees above 20°C, most species prefer a temperature between 0 and 6°C (BOCOCK & HEATH, 1967; WEGENSTEINER, 1982). Consumption and carbohydrate metabolism decrease above 25°C (BECK & FRIEBE, 1981; STRIGANOVA & RACHMANOV,1972).

Because of this dependence on temperature, it is difficult to compare the present observations with other examinations of the assimilation efficiency in Diplopoda. While our data largely agree with those measured for Iulidae by GERE (1956), KAYED (1978), and KONDEVA (1980), higher values for iulid species were observed under higher temperature and different food conditions

(Pokarzhevskii, 1981; Striganova & Rachmanov, 1972; Striganova & Valiachmedov, 1976).

As mentioned above the tendency towards a higher assimilation rate at a smaller body size by some arthropod taxa was confirmed for diplopods. Our data show distinctly that smaller animals such as *C. alemannicum* or *M. germanica* significantly assimilate more effectively than larger forms such as Iulidae or Glomeridae. Even within the Iulidae, the assimilation efficiency clearly decreases with increasing size (*C. silvarum* > *J. scandinavius* > *O. rutilans* > *T. albipes*). An increased metabolism of smaller arthropods was already assumed by Berthet (1971), and was confirmed for the assimilation rate of diplopods (Kondeva, 1980; Striganova, 1972).

This effect may result from a more effective digestion due to a better mastication of the ingested litter. The relative surface area of the food particles increases with smaller size caused by finer grinding. Thus digestive enzymes can more easily attack the ingested material.

Since the teeth of the pectinate lamellae are most likely responsible for the size of the ingested food particles, as recently assumed by Köhler & Alberti (1990) and confirmed by the present observations of the faeces by SEM, the density of these size-determining structures may be taken as a substitute for the food particle's size. Thus the linear correlation between the density of the teeth on the pectinate lamellae and the assimilation efficiency confirms the mentioned dependence. This relation, however, is not the only parameter determining assimilation. The enzymatic equipment must be taken into consideration as well. Thus the deviating results obtained from *P. angustus* may reflect the presence of cellulolytic activity in this species (Beck & Friebe, 1981), which is ascribed to only few species of the soil macrofauna.

5. Acknowledgements

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The assimilation rates of 8 central European species from different diplopod families were measured by feeding with natural leaf litter. Furthermore, the fine structural features of the mandible's gnathal lobe and the faeces of the mentioned species were examined by SEM.

The average values of the assimilation rates show a linear dependence on the tooth density of the pectinate lamellae on the gnathal lobe. The teeth of the pectinate lamellae most likely determine the food size. The highest assimilation rate corresponds to the smallest size of litter particles. Within the examined species, the highest tooth density and the highest assimilation efficiency occur in the smallest animals.

Key words: Diplopoda, assimilation, mandible, gnathal lobe, pectinate lamellae, fine-structure.

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